VOLUME XI NUMBER 1

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

UNIVERSITY OF HAWAII LIBRARY
MAR 12 '51

Contents

YOUNGIA AMERICANA, A NEW SPECIES OF PHYLETIC SIGNIFICANCE, *Ernest B. Babcock* 1

CYTOTAXONOMIC STUDIES IN THE GENUS SORGHUM. II. TWO NEW SPECIES FROM AUSTRALIA, *E. D. Garber and L. A. Snyder* 6

EVIDENCE FOR THE HYBRID NATURE OF × LIATRIS CREDITONENSIS, *L. O. Gaiser* 10

MORTON EATON PECK, *Lincoln Constance* 22

REVIEWS: Ernst Gäumann, *Principles of Plant Infection* (H. N. Hansen); William Randolph Taylor, *Plants of Bikini and other Northern Marshall Islands* (George F. Papenfuss); C. R. Metcalf and L. Chalk, *Anatomy of the Dicotyledons* (Herbert L. Mason) 24

Published at North Queen Street and McGovern Avenue,
Lancaster, Pennsylvania

January, 1951

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Board of Editors

Herbert L. Mason, University of California, Berkeley, Chairman.
LeRoy Abrams, Stanford University, California.
Edgar Anderson, Missouri Botanical Garden, St. Louis.
Lyman Benson, Pomona College, Claremont, California.
Herbert F. Copeland, Sacramento College, Sacramento, California.
Ivan M. Johnston, Arnold Arboretum, Jamaica Plain, Massachusetts.
Mildred E. Mathias, Dept. of Botany, University of California, Los Angeles 24.
Bassett Maguire, New York Botanical Garden, N. Y. C.
Marion Ownbey, State College of Washington, Pullman.

Secretary, Editorial Board—Annetta Carter
Department of Botany, University of California, Berkeley
Business Manager—Richard W. Holm
North Queen Street and McGovern Avenue, Lancaster, Pennsylvania
or
Natural History Museum,
Stanford University, California

Entered as second-class matter October 1, 1935, at the post office at Lancaster, Pa., under the act of March 3, 1879.

Established 1916. Published quarterly. Subscription price $4.00 per year. Completed volumes I to VIII, $5.00 each; volume IX, $6.00; volume X, $7.00; single numbers $1.00.

Manuscripts submitted for publication should not exceed 20 pages when printed nor contain more than 20 per cent illustrative material unless the author agrees to bear the additional costs. Range extensions and similiar notes will be published in condensed form with a suitable title under the general heading "Notes and News." Articles may be submitted to any member of the editorial board. Manuscripts may be included in the forthcoming issue provided that the contributor pay the cost of the pages added to the issue to accommodate his article. Reprints of any article are furnished at a cost of 4 pages, 50 copies $7.67; 100 copies $8.43; additional 100's $1.59; 8 pages, 50 copies $11.13; 100 copies $12.35; additional 100's $2.44; 16 pages, 50 copies $15.61; 100 copies $17.48; additional 100's $3.74. Covers 50 for $4.72; additional covers at $2.84 per hundred. Reprints should be ordered when proofs are returned.

Published at North Queen Street and McGovern Avenue, Lancaster, Pennsylvania, for the

CALIFORNIA BOTANICAL SOCIETY, INC.

President: George F. Papenfuss, University of California, Berkeley, California. First Vice-President: Lyman Benson, Pomona College, Claremont, California. Second Vice-President: Annetta Carter, University of California, Berkeley, California. Secretary: Phyllis G. McMillan, Department of Botany, University of California, Berkeley, California. Treasurer: Richard W. Holm, Natural History Museum. Stanford University, California.

Annual membership dues of the California Botanical Society are $4.00, which includes a year's subscription to Madroño. For two members of the same family the dues are $5.00, which includes one copy of Madroño and all other privileges for both. Dues should be remitted to the Treasurer. General correspondence and applications for membership should be addressed to the Secretary.

YOUNGIA AMERICANA, A NEW SPECIES OF PHYLETIC SIGNIFICANCE

ERNEST B. BABCOCK

A single specimen, collected last year in northwestern Alaska, is of unusual interest for several reasons. Although the plant is reminiscent of *Crepis nana typica* in its tufted habit and dark green, glabrous foliage, yet its most distinctive features are those of either *Soroseris* or *Youngia,* both of which genera hitherto have been restricted to Asia in their natural distribution (*Y. japonica* has been introduced as a weed widely in tropical regions). Since this plant combines certain characters of two Asiatic genera, it presents a problem in classification, especially in view of the absence of mature achenes. Immature achenes, however, are present, and a critical comparison of the material available with species of both genera provides a sound basis for classification. It appears certainly to belong in Section 1, *Desiphylum,* of the genus *Youngia,* near *Y. conjunctiva.*

Youngia americana sp. nov. Herba perennis valde humilis viridissima glabra; caulis subterraneus rectus tenuis cataphyllis triangularibus vestitus basi crassus cavus dense foliosus; folia caudicalia 2–7 cm. longa spathulata vel pinnatifida, ea caulina elongata tenuissima; caules aerei numerosi 4 cm. longi dense ramosi; capitula numerosa parva congesta 11–13-flora; involucrum cylindricum squamis exterioribus 3–4 linearibus eis interioribus 7 lanceolatis; corolla 10 mm. longa tubo 4.5 mm. longo glabro; antherae 2.5 mm. longae flavae; rami styli fusci 1.5–2 mm. longi; achenia (immatura) 2–3 mm. longa 11–13-costata costis 5 quam ceteris latioribus; pappus albus 6–7 mm. longus.

Perennial, tufted, ca. 3 cm. high, 12 cm. wide, dark green, glabrous; caudex ca. 3 cm. long, gradually broadened upward to 1 cm. in width including the leaf bases, hollow, terminating a slender vertical subterranean stem bearing cataphylls; longest caudical leaves, forming a rosette, ca. 7 cm. long, 1.4 cm. wide, the stout reddish petiole equal to the blade, lanceolate, pinnatifid, with narrow remote oblong-acute or triangular segments, dark green on upper face, yellowish on lower face, the margin retrorsely revolute; lowest caudical leaves 2 cm. long, spatulate, with oblanceolate blade 6 mm. long, 2 mm. wide; cauline leaves similar to the rosette leaves but reduced, with narrow elongated apical segment, the longest ca. 4 cm. long, the others 1–2 cm. long, filamentous; flower stems numerous, ca. 4 cm. long including the heads, reddish toward the base, paniculately closely branched, bearing ca. 6 heads on short slender peduncles; heads small, numerous, congested, 11–13-flowered; involucre cylindric, ca. 9 cm. long, 3.5 cm. wide at middle; outer bracts 3 or 4, narrow, terete,

---

MADROÑO, Vol. 10, No. 8, pp. vi, 225–256. November 10, 1950.

arcuate, ¼–½ as long as the inner ones; inner bracts 7, slightly coalesced at the base, in two ranks, outer ones 1.3 mm. wide, with a low thickened median protuberance near the apex, inner ones 2–2.5 mm. wide, broadly scarious-margined, shortly white-ciliate at the apex, glabrous on inner face; corolla 10 mm. long, the tube 4.5 mm. long, glabrous; ligule 2 mm. wide, the teeth 0.5–1 mm. long, prominently crested, dark brown *in sic.;* anther tube yellow, 2.5 mm. long, 1 mm. wide when opened out, the appendages 0.5 mm. long, linear, acute or acuminate, the filaments 1 mm. longer; pollen grains echinolophate, ca. 32 μ in diameter, the spines ca. 3 μ and similar to *Y. conjunctiva;* style branches dark brown, 1.5–2 mm. long, 0.1 mm. wide, the barbs not as prominent as in *Y. conjunctiva;* achenes (immature) pale tawny, 2–3 mm. long, 0.6–0.8 mm. wide, somewhat obcompressed, fusiform, constricted below the expanded pappus disk, 11–13-ribbed, the ribs unequal with 5 much stronger ones; pappus white, tinged yellowish at the base, 6–7 mm. long, 4-seriate, the setae nearly equal in length, unequal in width, the coarsest ones 50–60 μ wide at base, stiff but pliable, persistent. Flowering July, flowers yellow, anther tube yellow, stigmas dark brown.

Northwest Alaska, between latitude 68° 30′ and 69° 30′ N., along the Kukpowruk River. June–July, 1949 *Robert M. Chapman 132* (U. S. Nat. Herb. no. 1973474). According to Dr. Ira L. Wiggins (*in litt.*) Mr. Chapman made his collections almost entirely along the middle portion of the Kukpowruk River during his field stay in that part of Alaska.

This new species resembles either *Youngia* or *Soroseris* more than *Crepis* in its hollow caudex, its elongated, filamentous upper cauline leaves, the revolute margins of the caudical leaves, and in several features of the involucres, corollas, styles and achenes. Furthermore, the pollen grains in particular are like those of *Youngia conjunctiva* and very different from those of *Crepis nana.* The pollen grains of two species of *Soroseris* and of *Crepis sibirica* (a primitive species) and *C. tectorum* (a more advanced species) are illustrated in the monograph on *Dubyaea* and *Soroseris* (Stebbins, 1940, pp. 29–30). The pollen of *Y. americana* is similar to that of *C. sibirica. Soroseris* pollen is orange in color, becoming greenish blue when stained with cotton blue in lactophenol; whereas the pollen of *Y. conjunctiva, Y. americana* and *Crepis nana* is yellow and stains a bright, clear blue. The data on diameter of the grains and length of the spines for pollen of *S. Hookeriana erysimoides, Y. conjunctiva* and *Y. americana* are given in Table 1. In *Crepis nana* it was found that the pollen is much smaller than in the two *Youngia* species, being only 27 μ in diameter, and that the grains are devoid of spines, the surface being merely rugose.

Table 1 is a synoptical comparison of eleven morphological features and one anatomical character of *Y. americana* with those

TABLE I. SYNOPTICAL COMPARISON OF Y. AMERICANA WITH SOROSERIS AND YOUNGIA

	SOROSERIS	Y. AMERICANA	YOUNGIA
Stem	Usually short, thick and often hollow above ground, arising from a long rootstock	Short above ground, gradually thickened, hollow, arising from a rootstock	Long, or short in tufted species, but in the latter not notably thickened, borne on a rootstock
Cataphylls	Present on stem below rosette leaves	Present on stem below rosette leaves	Absent
Rosette leaves	Rarely pinnatifid, the margin not revolute	Pinnatifid, the margin revolute	Usually pinnatifid, the margin often revolute
Cauline and uppermost leaves	Gradually reduced, uppermost elongated, linear	Gradually reduced, the uppermost elongated, linear	In tufted species bractlike or resembling reduced rosette leaves
Outer bracts	2 (or 3-4), narrowly linear, shorter than or exceeding inner bracts	3, narrowly linear, ¼ - ½ as long as inner ones	Few, very short or up to ½ or 2/3 the inner, mostly lanceolate or deltoid
Inner bracts	4-15, lanceolate or ovate, not crested, somewhat coalescent at base	7, lanceolate, not crested but the median nerve or keel definitely thickened near the apex, coalesced only at the base	6/12, mostly 8, lanceolate, sometimes crested, carinate and thickened in fruit, not coalescent at base
Corollas	Ligulate, yellow or white, often blackish at base of ligule, 8-21 mm. long, the tube about ½ the total length (in one species 1/3)	Ligulate, yellow, 10 mm. long, the tube nearly ½ the total length	Ligulate, yellow, sometimes reddish on ligule, 5-22 mm. long, the tube mostly 1/5 to 1/3 the total length
Pollen grains	Subechinolophate or echinate, the spines large. In *S. Hookeriana* grains average 40μ in diam., spines 6-8μ	Echinolophate, the spines similar to *Y. conjunctiva*. Grains average 32.5μ in diam. spines ca. 3-4μ	Echinolophate, the spines variable but smaller than in *Soroseris*. In *Y. conjunctiva* grains aver. 31μ in diam., spines ca. 5μ
Style	Blackish or greenish, stigmatic branches 1-3.5 mm. long, 0.2-0.3 mm. wide, the barbs on outer surface numerous, close, prominent	Brown (in. sic.), branches 1.5-2 mm. long 0.1 mm. wide, the barbs on outer surface similar to *S. umbrella* but not quite as prominent as in *Y. conjunctiva*	Yellow or sometimes brown branches 0.5-2.5 mm. long, 0.05-0.1 mm. wide, the barbs ranging from very fine to rather prominent
Achenes	Oblong or more attenuate toward base, constricted at apex, slightly obcompressed, many-striate	Immature achenes fusiform or oblong, ± obcompressed, 10-13 ribbed, the ribs unequal with 5 much stronger ones	Fusiform or oblong, obcompressed (sometimes strongly), with 3-5 stronger ribs
Pappus	7-16 mm. long, white, stramineous, yellow, gray, dusky or rufescent; the setae very numerous, coarse, stiff	6-7 mm. long, white; the setae 4-seriate, resembling *Y. conjunctiva*	2-11 mm. long, white, yellow, gray or fuscous; the setae rather coarse, stiff and brittle to fine or very fine and soft
Ovary anatomy	Primitive, numerous supernumerary strands	Advanced, no supernumeraries	Advanced, no supernumeraries observed in two species

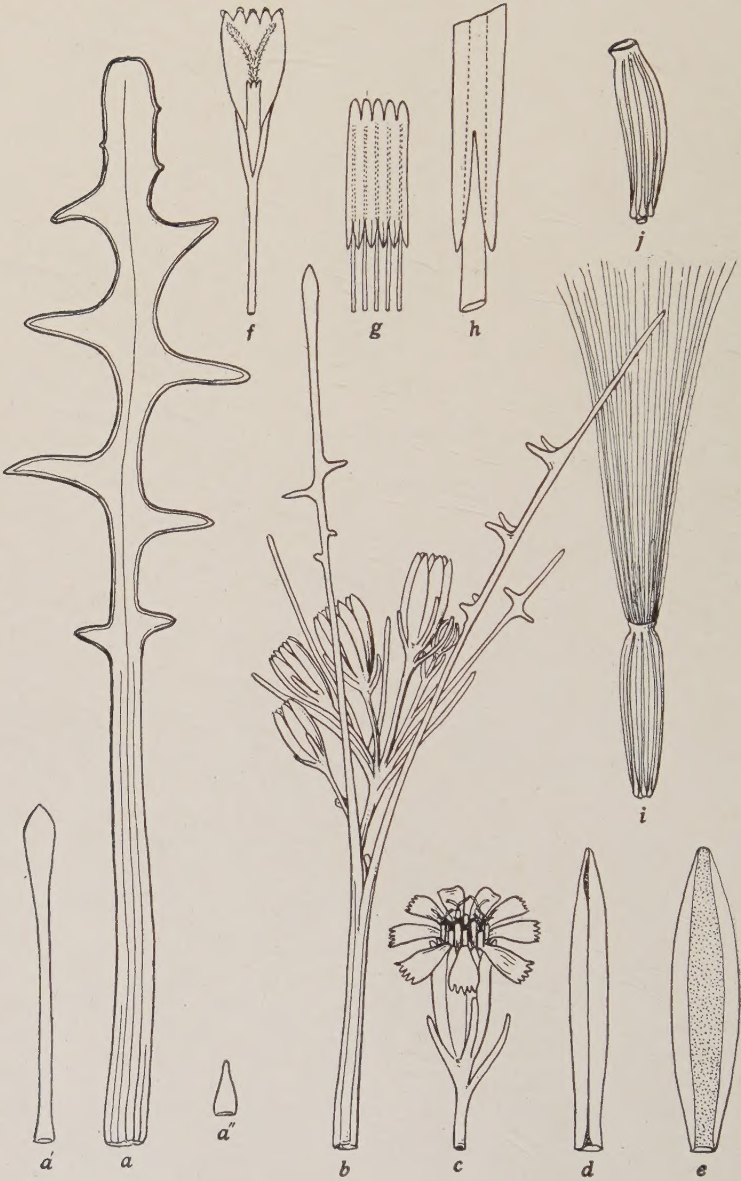


Fig. 1. *Youngia americana* Babcock. From the type: *a*, rosette leaf, lower face, *a′*, lowest caudical leaf, *a″*, cataphyll, × 2¼; *b*, flower stem, × 2; *c*, head in anthesis, × 2; *d*, *e*, inner involucral bracts from outer and inner series, outer face, × 4; *f*, floret lacking ovary, × 4; *g*, anther tube opened out, × 8; *h*, detail of appendage, × 32; *i*, marginal achene (immature, pappus removed), × 8; *j*, inner achene with pappus, × 8. (Drawings by the author, inking by Miss Anna Hamilton.)

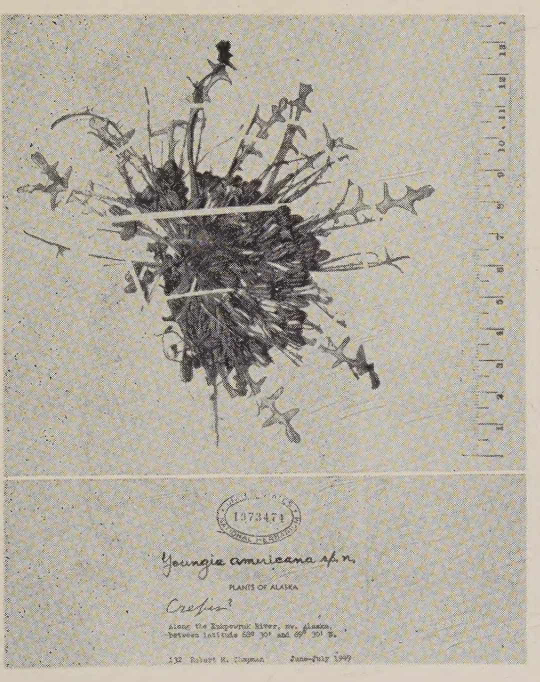


FIG. 2. *Youngia americana* Babcock. Type specimen in United States National Herbarium, folio no. 1973474. (Photograph by V. Duran.)

of both *Soroseris* and *Youngia*. It will be noted that the distinctive resemblances to the two genera are about equal in number, five for *Soroseris* and seven for *Youngia;* but that the *Soroseris* resemblances are found mostly in vegetative features, whereas most of the resemblances to *Youngia* occur in the pollen grains, the style and stigma, the immature achenes, the pappus, and especially the ovary anatomy. The peculiarities of the styles and pollen grains and the presence of numerous supernumerary strands in the ovary are considered the most distinctive features of *Soroseris* (Stebbins, 1940). Since it is in these parts of the plant, as well as in the achenes, that this new species shows definite resemblance to *Youngia,* its classification in the latter genus is clearly indicated.

At the same time, the hollow caudex, the cataphylls on the rootstock below the rosette leaves, the elongated linear upper cauline leaves, the few, long, linear outer involucral bracts, and the long corolla tube, are not found in most species of *Youngia,* whereas they are characteristic of most *Soroseris* species. This occurrence of *several* marked resemblances to *Soroseris* appeals to the author as indicating affinity with that relict genus of the Sino-Himalayan region (Stebbins, 1940), thus endowing this plant with considerable phylogenetic significance. As in the case of *Crepis pygmaea* which, in certain features, exhibits resemblance to *Youngia depressa,* while the latter species in turn shows relationship with the more primitive genera, *Soroseris* and *Dubyaea,* so in *Y. americana* we find additional evidence that *Youngia* and *Soroseris* had a common derivation. The ancestral group from which *Youngia, Crepis,* and the other genera of the Crepidinae were probably derived is the genus *Dubyaea* (Stebbins, 1940; Babcock, 1947).

These clearly indicated phylogenetic relations have a direct bearing on the location of the center of origin of the Crepidinae. Extensive evidence has already been presented (cf. Babcock, 1947, Pt. I, Ch. 6, especially pp. 96–97) that both *Soroseris* and *Dubyaea* originated in central Asia and migrated southeast and south to their present areas of distribution. The discovery of this primitive species of *Youngia* in Alaska suggests a similar origin and migrational history to that of *Crepis,* section *Ixeridopsis.* In addition to this section, all of the other native American species of *Crepis* were unquestionably derived from species or hybrids that must have migrated across Beringea in Tertiary times. This evidence, together with the well justified assumption (Babcock, 1947, pp. 108, 137–139) that some of the *Crepis* species of northern Europe and of Iceland (*C. paludosa*) or their ancestors migrated westward south of the Ural Mountains in early Miocene, points to a northern central Asiatic origin of *Crepis.* Now, in *Youngia americana,* we find additional support for the concept of a northern Asiatic origin of the Crepidinae.

Division of Genetics
University of California, Berkeley

Literature Cited

Babcock, E. B. 1947. The genus Crepis. Univ. Calif. Publ. Bot. 21.

Stebbins, G. L., Jr. 1940. Studies in the Cichorieae: Dubyaea and Soroseris, endemics of the Sino-Himalayan Region. Bull. Torrey Club 19: 5–76.

CYTOTAXONOMIC STUDIES IN THE GENUS SORGHUM.
II. TWO NEW SPECIES FROM AUSTRALIA

E. D. Garber and L. A. Snyder

In a recent taxonomic revision of the genus *Sorghum,* Garber (1950) recognized six subgenera: *Eu-Sorghum, Chaetosorghum, Heterosorghum, Sorghastrum, Para-Sorghum,* and *Stiposorghum.* Among the subgenera, *Para-Sorghum,* and *Stiposorghum* form one circle of affinity and the other subgenera constitute a second circle of affinity.

The basic chromosome number of *Sorghum* is 5 and is known only in *Para-Sorghum* and *Stiposorghum.* The application of cytological methods to the taxonomic problems of this genus and especially of the subgenera *Para-Sorghum* and *Stiposorghum* has been eminently successful. A cytological study of a collection of Australian sorghums, using criteria previously validated in defining species of these subgenera, has revealed the presence of two undescribed species.

Materials and Methods

Herbarium specimens of Australian sorghums furnished by

Mr. S. T. Blake, Botanic Gardens, Brisbane, Queensland, yielded a small number of seed which were planted in Berkeley, California. For cytological study, immature panicles were fixed in a fresh solution of absolute alcohol and glacial acetic acid (3:1) for 24 hours and then transferred to 70 per cent alcohol for storage. Pollen mother cell smears were stained with acetocarmine.

TAXONOMY

Specimens number 17526 and 17536 of Blake's collections were identified as *Para-Sorghum* and *Stiposorghum,* respectively, but could not be identified as any known species. An examination of the meiotic chromosomes gave additional evidence of the distinctiveness of these collections.

Sorghum australiense sp. nov. Planta annua, culmorum nodis dense barbatis, ramis primariis verticillatis plerumque simplicibus, pulvino parvo, spicularum sessilium callo obtusissimo spiculis sessilibus 7.0–8.5 m. longis, aristis 35–48 mm. longis, lodiculis glabris cupuliformibus crassis, spiculis pedicellatis masculinis vel neutris 6.5–8.0 mm. longis, fructu obovato. Chromosomae 2n = 20.

Annual; nodes of the culms, at least the upper, bearded; primary branches of the panicle whorled, usually simple; callus of the sessile spikelets obtuse; pulvinus not prominent; sessile spikelets 7.0–8.5 mm. long, brown; awns 35–48 mm. long; lodicules glabrous, cup-shaped, thick; pedicelled spikelets staminate or neuter, lacking lemmas, 6.5–8.0 mm. long; mature caryopsis obovoid. Chromosomes 2n = 20.

Type. East of Mataranka, near Elsey Station, Northern Territory, Australia, April 29, 1947, *S. T. Blake 17526* (Herbarium, Botanic Gardens, Brisbane, Queensland).

Sorghum australiense is the first annual *Para-Sorghum* found east of India. The other annual species in the subgenus, *S. purpureo-sericeum* and *S. versicolor,* are restricted to western India and eastern Africa.

The glabrous, cup-shaped, thick lodicules of *S. australiense* are unique among the species of *Para-Sorghum* that have been examined. Pilger (1940), however, has placed *S. trichocladum,* a species with glabrous lodicules occurring in western Mexico and northern Guatemala, in the subgenus *Para-Sorghum.* Until living material of this species is available for cytotaxonomic study, this disposition cannot be verified. Within the subgenus, only *S. versicolor* has longer awns than *S. australiense.* Of the five species of *Para-Sorghum,* the three annual species have relatively long awns (27–54 mm.), and the two perennial species, short awns (12.5–24.0 mm.).

More than 200 spikelets of an open pollinated plant of *S. australiense* were examined and yielded no seed. Until extensive populations are available for hybridization, it is not possible to decide whether sterility is due to self-incompatibility as in *S. leiocladum,* a tetraploid species of *Para-Sorghum,* or to environmental factors. Using stainability with cotton blue in lactophenol as a criterion of pollen viability, approximately 80 per cent of the pollen grains appear to be functional.

Sorghum matarankense sp. nov. Planta annua culmorum nodis dense barbatis, ramis primariis verticillatis plerumque simplicibus, pulvino parvo, spicularum sessilium callo acuminato 1.0 mm. longo, spiculis sessilibus 6.0–6.5 mm. longis, lodiculis ciliolatis membranaceis, spiculis pedicellatis masculinis 6.0–7.0 mm. longis, fructu late subulato. Chromosomae 2n = 10.

Annual; nodes of the culms, at least the upper, bearded; primary branches of the panicle whorled, usually simple; pulvinus not prominent; callus of the sessile spikelets pointed, 1.0 mm. long; sessile spikelets 6.0–6.5 mm. long, brown; awns 35–50 mm. long; lodicules ciliate, membranaceous; pedicelled spikelets staminate, 6.0–7.0 mm. long; mature caryopsis broadly subulate. Chromosomes 2n = 10.

Type. East of Mataranka, near Elsey Station, Northern Territory, Australia, April 29, 1947, *S. T. Blake, 17536* (Herbarium, Botanic Gardens, Brisbane, Queensland).

The short, pointed callus of the sessile spikelets in *S. matarankense* is also found in *S. brevicallosum* and serves to distinguish these species from the others in *Stiposorghum.* The shorter sessile spikelets, 6.0–6.5 mm. compared with 7.5–8.5 mm., and longer awns, 40–50 mm. compared with 38–43 mm. distinguish *S. matarankense* from *S. brevicallosum.* The very short hairs of the bearded nodes in the former species contrasts with the long hairs of the bearded nodes in the latter species. The primary branches, especially in the lowermost whorls, are usually divided, a character not yet observed in any species of *Stiposorghum.* Similar to the situation in *Para-Sorghum,* the one known perennial species in *Stiposorghum, S. plumosum,* has short awns (28–50 mm.) compared with the four known annual species (38–85 mm.).

From more than 200 spikelets of an open pollinated plant of *S. matarankense,* no seed was obtained. Whether this sterility is due to self-incompatibility or environmental factors is not known. This observation, however, is not unexpected since the species of *Stiposorghum* are characteristically self-incompatible.

CYTOLOGY

Sorghum australiense with a somatic chromosome number of 20 is a tetraploid. Since two plants had different numbers of rings of four chromosomes at diakinesis and metaphase I of meiosis, it is not possible to decide whether this species is an allotetraploid or autotetraploid. At any rate, the three Australian species of *Para-Sorghum* are tetraploids and the two African species, diploids. Since the three Australian species are either autotetraploid or allotetraploid, there is reason to believe that additional collections of *Para-Sorghum* from Australia may yield diploid species.

The meiotic chromosomes of *S. australiense* are similar in morphology to those of the other species of the subgenus at pachytene, diakinesis, and metaphase I. The chiasmata frequently at diakinesis and metaphase I was determined for one plant, A50/3–4. It had up to four rings of four chromosomes at these stages. Consequently, the data on chiasmata frequency had to be expressed as the mean number of half chiasmata per chromosome. At diakinesis, the mean number of half chiasmata per chromosome was 1.90 (26 PMC's) compared with 1.58–2.42 for the other species of *Para-Sorghum,* and at metaphase I, 1.79 (25 PMC's), compared with 1.50–2.04 for the other species.

Approximately 50 per cent of the pollen mother cells (26 of 50 PMC's) had more than one nucleolus at pachytene; two pollen mother cells had three nucleoli at the same stage. The nucleolus organizing region was heteropycnotic; the nucleolus chromosome in cells with only one nucleolus was associated with the nucleolus at an intercalary position, thus distinguishing this species from the other two tetraploid species with terminal nucleolus organizing regions.

Sorghum matarankense with a somatic chromosome number of 10 is the fourth diploid species of *Stiposorghum.* The meiotic chromosomes at pachytene, diakinesis, and metaphase I are similar in morphology to the chromosomes of the other species of *Stiposorghum* at the same stages. The mean number of chiasma per chromosome at diakinesis was 0.61 (40 PMC's) compared with 0.55–0.60 for the other diploid species, and at metaphase I, 0.60 (27 PMC's), compared with 0.52–0.55 for the other diploid species. The percentage of bivalents with one chiasma at diakinesis was 78 per cent (40 PMC's), and at metaphase I, 80 per cent (27 PMC's) compared with 78.9–88.9 per cent and 89.0–96.0 per cent for the other diploid species at the respective stages.

Two of the five bivalents in *S. matarankense* were associated with one nucleolus at pachytene, an observation typical of the diploid species of *Stiposorghum.* The position of the nucleolus organizing region was determined for each chromosome. In one chromosome, the nucleolus organizing region was terminal, and in the other, subterminal; the former chromosome was noticeably shorter than the latter at pachytene. The presence of a terminal nucleolus organizing region suffices to distinguish *S. matarankense* from the other diploid species of *Stiposorghum* in which none of the nucleolus organizing regions is terminal.

Summary

Cytotaxonomic methods have been indispensable tools for arriving at conclusions as to taxonomic relationships and evalua-

tion within the complex genus *Sorghum*, especially in the subgenera *Para-Sorghum* and *Stiposorghum*.

The authors wish to acknowledge with gratitude the cooperation of Mr. S. T. Blake, Botanic Gardens, Brisbane, Queensland, who provided herbarium specimens of the Australian sorghums. We are also indebted to Dr. G. L. Stebbins, Jr., Division of Genetics, University of California, for field and greenhouse facilities.

Division of Genetics,
University of California, Berkeley,
and Department of Plant Sciences,
University of Oklahoma, Norman.

LITERATURE CITED

GARBER, E. D. 1950. Cytotaxonomic studies in the genus *Sorghum*. Univ. Calif. Publ. Bot. 23: 283–362.

PILGER, R. 1940. Gramineae, III: Unterfam. Panicoideae in Engler u. Prantl, Die naturlichen Pflanzenfamilien, 2^2, Bd. 14e. Engelmann. Leipzig. 208 pp.

EVIDENCE FOR THE HYBRID NATURE OF X LIATRIS CREDITONENSIS

L. O. GAISER

This paper[1] is concerned with a plant described by the author (1946) as a putative hybrid between *Liatris ligulistylis* and *L. squarrosa* var. *glabrata*, under the name of × *L. creditonensis*. Because of the practical difficulty of controlled breeding of Compositae, it has not been possible to demonstrate the hybrid nature of × *L. creditonensis* by planned resynthesis. The available evidence that it is a hybrid is here presented.

Liatris ligulistylis (Nels.) K. Sch. has a known range of the three prairie provinces of western Canada and southward along the eastern side of the Rocky Mountains through western South Dakota, Wyoming, and Colorado into northern New Mexico. It favors comparatively moist habitats. *Liatris squarrosa* (L.) Michx. var. *glabrata* (Rydb.) Gaiser on the otherhand is found on the dry open plains from Kansas to South Dakota. The ranges of these two entities do not overlap.

A garden plot of thirty-two plants of *L. squarrosa* var. *glabrata* (Accession No. 9) planted in 1928 from seed collected in Nebraska (high cliff northwest of Royal, Antelope County, 4 October 1927, *Wernicke*) developed into uniform, one-stemmed plants during their second year of growth, and by 1933 when they were five years old they had become several stemmed (Pl. 1, fig. 1). Growing beside this plot were two plants of *L. ligulistylis* (Accession No. 1) which had been collected in Minnesota (near Erskine, Polk County, August, 1929, *Gaiser*). One was atypical in being more paniculate and in having more elongated basal peduncles than is usual in the species (Pl. 1, fig. 2).

---

[1] The author is indebted to Dr. R. Rollins and E. Anderson for reading the manuscript and to the latter also for suggesting Fig. 2.

Although stray seedlings were normally weeded out from the plots, one which was growing at the side of the bed of *L. squarrosa* var. *glabrata* and next to the two plants of *L. ligulistylis* was allowed to persist. In 1932 this plant (No. 52) bloomed and was seen to be intermediate between those two entities (Table 1), although the influence of *L. squarrosa* was more pronounced. This plant (Pl. 1, fig. 3) proved to be the supposed hybrid, × *L. creditonensis.*

Because phyllaries show a wide variation in form and were considered important in distinguishing closely related species within a series, it was hoped that from the recombinations of their characters in this plant (No. 52), some knowledge of its parentage might be gained. In the phyllaries of plant No. 52, the characters of *L. ligulistylis* and *L. squarrosa* var. *glabrata* were combined even more that it was possible to indicate in Table 1.

Cytological Observations

Chromosome counts from pollen mother cells of *L. squarrosa* var. *glabrata* (No. 9) were $n = 10$ (fig. 1 a–d) and from seedling root tips, $2n = 20$. Meiotic figures (fig. 1, e, f) of *L. ligulistylis* (No. 1) appeared very similar to those of *L. squarrosa* var. *glabrata*. In the putative hybrid (No. 52) first metaphase plates showed ten chromosomes (fig. 1, g, h). A study of numerous lateral and polar first metaphase figures showed that there was always regular pairing of the bivalents. The anaphase and telophase proceeded regularly; at second metaphase (fig. 1, i, j), the uniformity of the chromosome plates was striking. There were no lagging chromosomes; second telophases and pollen tetrads were perfectly formed. Because of the similarity of the meiotic chromosomes of the two putative parental species, however, the form and number of the chromosomes was of little help in determining the origin of seedling No. 52.

Progeny of × l. creditonensis No. 52

The putative hybrid (No. 52) was partially fertile when open-pollinated. A number of achenes were obtained the first year that the plant was observed in bloom. Since the seeds were sown late in the season, many of the seedlings did not have time to develop a sufficiently thick corm to survive the winter. Thus, the fact that only fifteen strong seedlings were available for transplanting in the spring is not necessarily indicative of the vitality of the lot.

In September 1934, the seedlings were in their second year and most of them had come into bloom. Two of them with narrower, more rigid, declined and somewhat twisted rather than broader upright leaves, and with projecting phyllaries were very much like *L. squarrosa*. Three of them more closely resembled the parent plant No. 52 in their wider, somewhat erect leaves. However, these three were not alike in their phyllaries, two of them again having the more outspread phyllaries like *L. squarrosa* and one having phyllaries similar to those of its parent. Thus, progeny of the putative hybrid showed various recombinations of the characters of *L. squarrosa* and *L. ligulistylis*.

With regard to seven characters, the progeny were compared with the seed parent and with the two original species. Most of the progeny were nearly like the seed parent. Three were quite like *L. squarrosa*, and eight more approached *L. squarrosa* in one character or another. None closely resembled *L. ligulistylis*.

At various times during the study, voucher specimens for deposit in the Gray Herbarium were taken from × *L. creditonensis*, from the putative parents and from the various progeny.

Cytological Examination of Progeny of Plant No. 52

Meiosis was studied in the pollen mother cells of one resembling *L. squarrosa* and of another resembling the seed parent. In both, divisions were normal with a regular arrangement of ten bivalents at first metaphase (fig. 1, k, l). Though many clear figures of all stages of the first and second divisions were seen, no lagging units on the spindles and no micronuclei were found. One count of eleven chromosomes on a second metaphase plate suggested irregularities (fig. 1, n) but was probably due to precocious splitting of one chromosome or to pressure on the mount. Slight pressure on the coverslip over first metaphase plates caused a similar elongation of a few of the bivalents as they were seen somewhat laterally (fig. 1, m). Study of a third plant during two different seasons showed only mature pollen which was very regular in form.

In 1934 seven of the progeny produced many good achenes, though one produced only six. From each of the seven, fifteen achenes were germinated for cytological examination of the root tips. The percentage of germination was good, varying from 40 to 86 in all except one which was not tested at the same time as the others and for which it was believed that temperature conditions were unfavorable. Of the plant which produced six achenes, all except one germinated. In 1935, achenes were col-

---

Explanation of the Figures, Plate 1.

Plate 1. Specimens of Liatris Grown in Garden. Fig. 1, Five year old seedling of *L. squarrosa* var. *glabrata* (No. 9 plant 32).—Fig. 2, *L. ligulistylis* (No. 1 plant 2).—Fig. 3, × *L. creditonensis* (No. 52) photographed 1933. All approximately × 1/7.

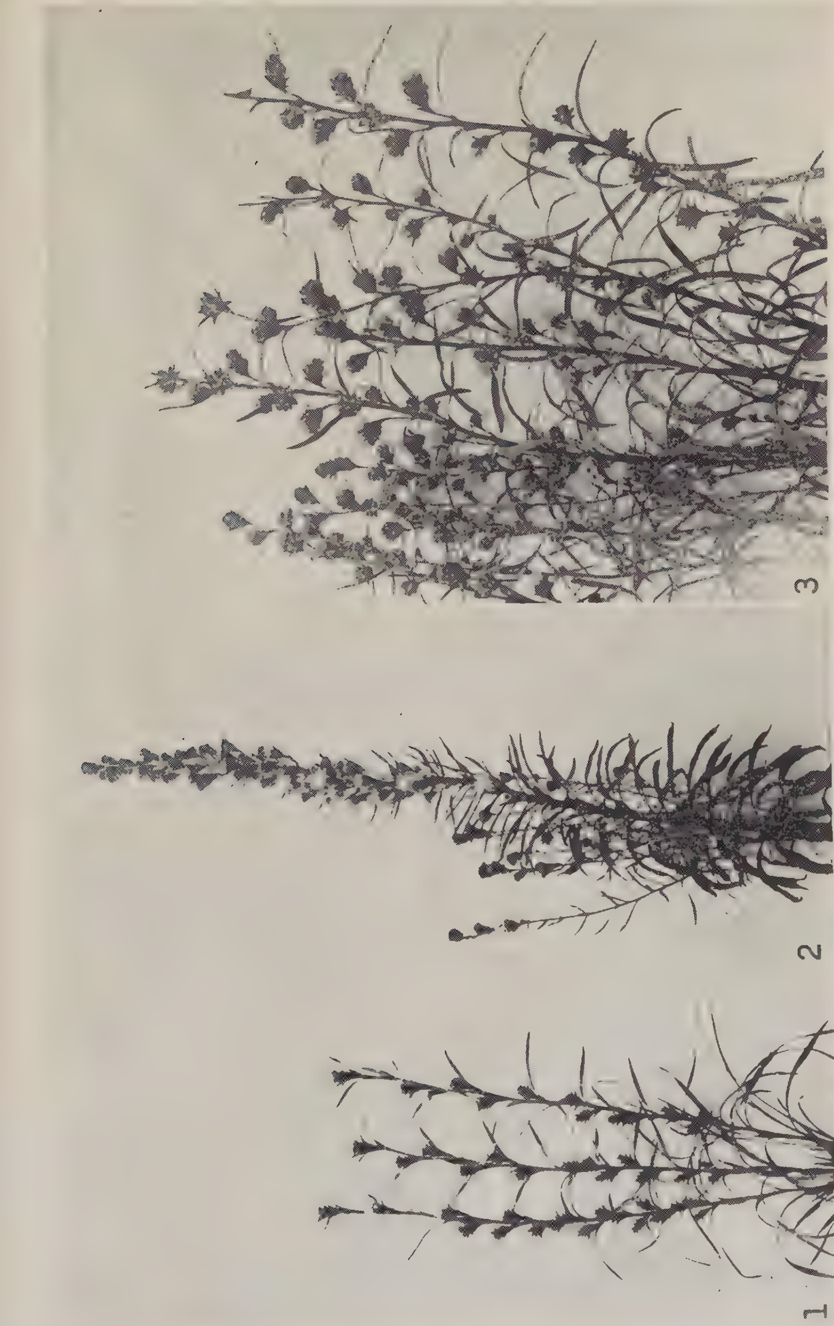
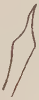
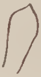
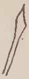
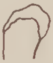
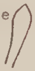


Plate 1. Specimens of Liatris Grown in Garden.

TABLE 1. COMPARISON* OF LIATRIS HYBRID WITH PUTATIVE PARENTS

	L. squarrosa var. glabrata No. 9	L. ligulistylis No. 1	X L. creditonensis No. 52
Corolla			
Color**	Mathews purple, 65	Lilac, 65d.	Lilac, 65d.
Length	12mm.	7-9mm.	9mm.
Shape	Erect to end of pappus and then flattened (rotate)	Erect, tubular	Erect, tubular
Lobes	Hairy	Glabrous	Slightly hairy
Style			
Length	20mm.	14mm.	18mm.
Color**	Mauvette, 65f.	Lilac, 65d.	Mauvette, 65f.
Pappus			
Length	7mm.	7-8mm.	8mm.
Nature	Plumose	Barbellate	Barbellate
Achene			
Length	6mm.	4-5mm.	6mm.
Phyllaries			
Color	All green	Green with reddish tips	All green
Nature	Glabrous, chaffy	Glabrous, membranous	Glabrous, not quite as chaffy as #9
Margin	No cilia, not scarious	Markedly scarious and lacerate	No cilia, not scarious
Position	Outspread	Erect, very slightly incurved	Mostly slightly incurved
Shape of outer ones	Sharply acuminate 	Broadly ovate and short	Elliptical acute, not sharply acute 
Size of outer ones	12mm. long	4-5mm. long	10-11mm.long, 3-4mm. wide
Shape of inner ones	Linear acute 	Broadly spatulate 	Linear, spatulate 
Length of inner ones	15mm. long	8mm. long	15mm. long
Peduncles	4-8mm. long	4mm.-12cm. (of basal flower)	20-25mm. long

* These observations were made at the time the styles were exserted, August 1933, with revision of pappus and achene lengths to those of mature conditions.

** Colors are according to Ridgway's Color Chart, plate XXV.

lected from eleven plants, of which five were other than those checked in the previous season. Though their viability was not tested, it is probable from the appearance of the well-filled achenes that their germination would have been as high. The somatic chromosome number was confirmed as twenty in six seedlings.

In numerous figures obtained from one seedling, at least two pairs of chromosomes were found to be longer than the rest, one pair long-median, and one pair sub-median. For the rest of the chromosomes, it was difficult to draw a line between those of intermediate length and the shortest ones.

Further Analyses of the Progeny

Using the hybrid index method of Anderson (1949), × *L. creditonensis* was compared with its putative parents and with its

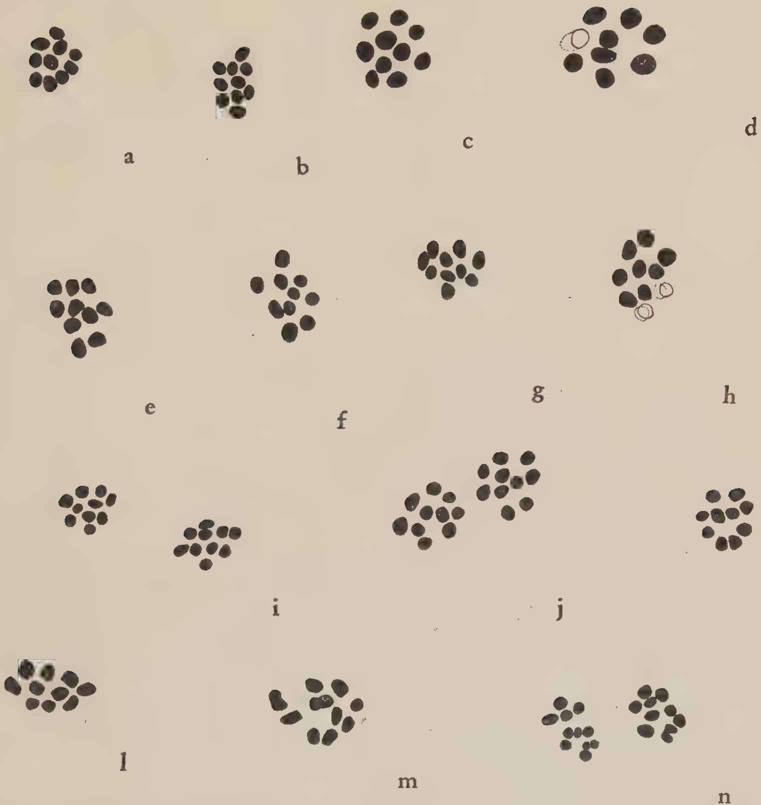


Fig. 1. Meiotic chromosomes of × *L. creditonensis* and the two putative parents as seen in polar views of first metaphase (except i, j, n which are second metaphase) in pollen-mother-cells from aceto-carmine preparations, drawn by Zeiss apochromatic lenses and camera lucida at aproximately ×1900. Figs. a–d, *L. squarrosa* var. *glabrata* No. 9 ($n=10$): *a, b,* two young seedlings in their first summer of bloom; *c, d,* seedling 32 in its fifth year. Figs. e, f, *L. ligulistylis* No. 1 plant 1 ($n=10$). Figs. g–j, × *L. creditonensis* No. 52 ($n=10$): *g,* drawn in 1932; *h–j* drawn in 1933. Fig. k, plant 8 of progeny of No. 52. Figs. l, n, plant 12 of progeny of No. 52.

progeny, nine diagnostic and measurable characters being studied from the herbarium material—pilosity of corolla limb; nature of the pappus (length of barbules); margin, shape, and position of phyllaries; shape, surface, and margin of leaves; and pubescence of upper stem (Table 3).

As to the first character considered, pilosity of the corolla limb, *L. squarrosa* has hairy corolla lobes, whereas *L. ligulistylis* has a completely clear corolla, lacking any pilosity within the limb, throat, or tube. This is in contrast not only to *L. squarrosa,* but also to other species of the *Scariosae* which have hairs within the throat. (In referring to parts of the corolla, the tube proper will here be regarded as the part below the insertion of the filaments, the part above that being referred to as the throat and limb, of which the latter refers to the teeth only.) In determining the hybrid index, *L. squarrosa,* with profuse hairs, was scored 4, × *L. creditonensis,* with few hairs, 1, and *L. ligulistylis,* with no hairs, 0. The progeny was scored from 1 to 4.

The second character considered was nature of the pappus. *L. squarrosa* has a very plumose pappus, whereas in *L. ligulistylis* the pappus is barbellate and to the naked eye not obviously plumose. As can be seen in those species of *Liatris* having a plumose pappus, the barbules toward the base of the seta are generally shorter. Also, as was noticed early by Cassini (1827) in *Suprago,* even along the mid portion of the seta there are differences in length of the barbules. Inasmuch as only the longest projecting barbules are readily distinguishable when setae are flattened under a cover slip, measurements were made only of these longer barbules. The figures, therefore, do not represent the full range of length. For each species, measurements were made of ten specimens from widely distributed localities. These included the isotypes and two plants of each of the accessions studied above. For each of these plants, twenty-five barbules were measured. In making these preparations, it was found that lactic acid was a satisfactory mounting medium for the short-barbuled setae of *L. ligulistylis,* but for the plumose setae of *L. squarrosa* parlodion proved to be better. Table 2 gives the means and standard errors of these measurements. Plant No. 52 falls between the two species, just at the upper limits of *L. ligulistylis.* This confirms the macroscopic determination of its pappus as barbellate (Gaiser, 1946). Only one of the progeny had a mean lower than that of the parent plants, and the rest fell between it and *L. squarrosa.* In determining the hybrid index, the barbule length of *L. ligulistylis* was scored as 0 and that of *L. squarrosa* as 2. Intermediate lengths were then scored fractionally.

For the other eight measurable and diagnostic characters studied, the condition of *L. ligulistylis* was scored 0, the intermediate condition 1, and the condition of *L. squarrosa* 2, except for pilosity of corolla limb which was scored from 0 to 4. Scoring and totals are shown in Table 3. Thus, with the putative parents having a total score of 0 and 20, plant No. 52 receives only a total of 10.44. The scores of the progeny fell between those of *L. squarrosa* and × *L. creditonensis,* the highest nearly approaching that of *L. squarrosa* and the lowest that of × *L. creditonensis,* none approaching closely to *L. ligulistylis.* This confirms the observations on the living plants, most being like the parent plant or intermediate between the latter and *L. squarrosa.* Independent segregation is shown, however, in some of the charac-

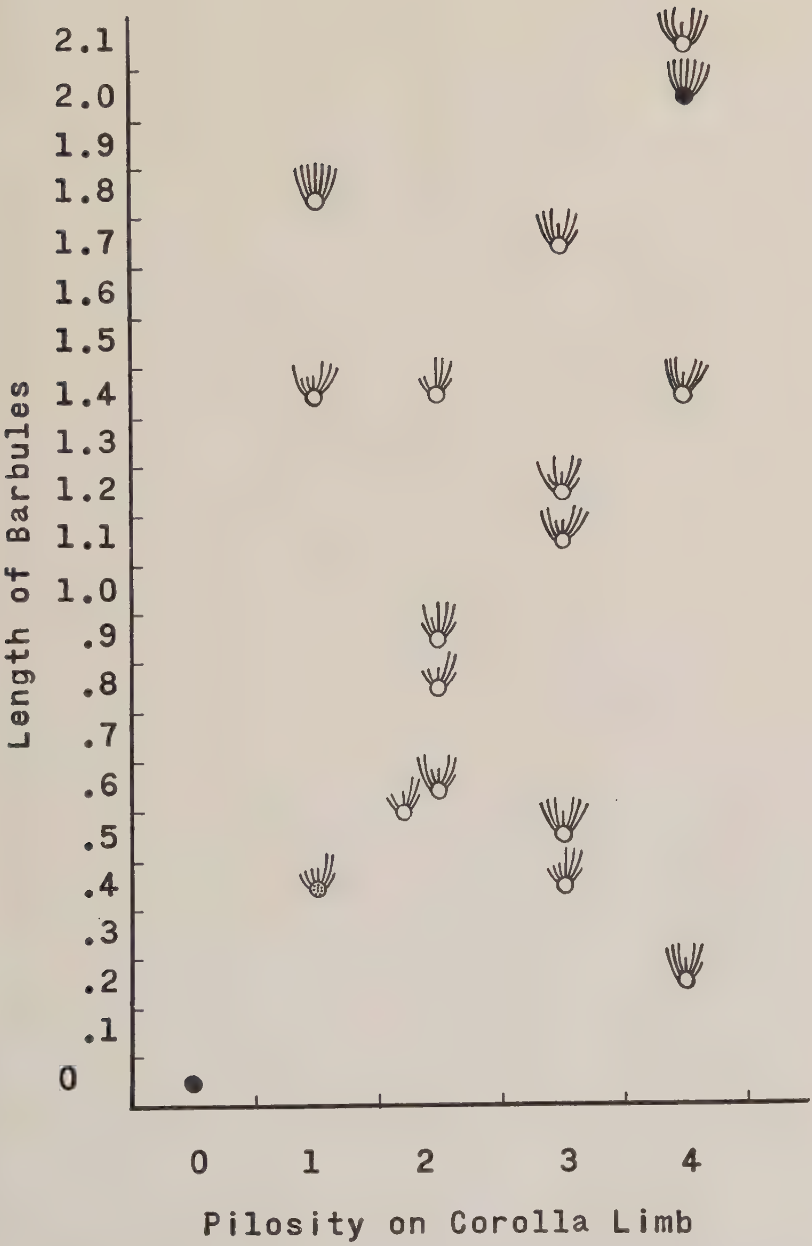


FIG. 2. Scatter diagram of progeny of × *L. creditonensis* (Plant No. 52): *L. ligulistylis* (black circle in lower left); *L. squarrosa* (black circle in upper right); *L. creditonensis* (stippled circle); the progeny (clear circles). From left to right the symbol arms represent the phyllary, leaf and stem characters in Table 3, long arms a score of 2, and half length, a score of 1.

ters. In the pictorialized diagram (fig. 2), the diversity of the progeny is at once apparent. On the basis of the characters scored, no two of them are exactly alike.

DISCUSSION

With the common observation of the intermediacy of an F_1 between the two parents, it is sometimes less well remembered how greatly the progeny of even an F_2 vary from one another. However, as Anderson (1949) has recently emphasized, the number of recombinations in an F_2 is not numerous considering the total possibilities in the multitudinous characters of two species. Because of the linkage of genes, as at least one limiting factor, fewer types of combination are achieved. Also as he has pointed out from the analysis of hybrid populations under natural conditions, there is a repeated backcrossing of the hybrids to one or both of the parents, and with each successive generation the hybrid nature is less apparent. The result is that a few resemble the recurrent parent and a few the F_1, but a larger proportion will be intermediate between these two.

In Plant 52 (× *Liatris creditonensis*) and its progeny, there was shown a change from the distinct intermediate plant No. 52 to some of its progeny. Because of the failure of some of the insufficiently developed seedlings to over-winter, the complete population could not be represented in the study. The fifteen progeny which were grown varied so slightly among themselves that when for lack of better characterization they were divided into seven categories, two were described as practically like the parent plant and eight were considered close to it but with other combinations of characters from the one contributing parent species *L. squarrosa*. While two categories were recorded at that time based on close similarity to *L. squarrosa,* none pointed singly to *L. ligulistylis*. The more extended analysis (Table 3), including measurements of two characters of a quantitative nature, confirm this. Though the total scores of the progeny range from those very nearly as low as the parent plant No. 52 to those very nearly as high as *L. squarrosa,* none at all had a score approaching *L. ligulistylis*. These plants seem to meet the situation described by Anderson of a backcross to the recurrent parent with *L. squarrosa* as that parent. As there was quite a bed of *L. squarrosa* (No. 9) seedlings (originally there had been thirty-two) it is logical to assume that there would be more pollen of that species available for pollination than of *L. ligulistylis,* of which there were only two plants. Because the hybrid was open-pollinated it is not known whether the seeds that were germinated were really the result of fertilization of those flowers by pollen of other flowers of the same plant or by pollen of plants of either or both of the other two species. Compatability of the chromosomes of either species could be expected in view

TABLE 2. MEAN LENGTH OF BARBULES OF PAPPUS

Specimens examined		Barbule length	Standard Error
*Liatris ligulistylis***		30.54	±.2820
Liatris squarrosa var. *glabrata***		92.37	±.5235
X *L. creditonensis*, No. 52		43.85	±.8708
Progeny of No. 52	Plant 6	35.85	±.8799
	" 2	43.85	±.8032
	" 4	45.25	±.6349
	" 7	47.05	±1.2291
	" 15	47.25	±.8216
	" 1	53.25	±1.1080
	" 9	55.05	±.7525
	" 8	59.25	±.7362
	" 5	63.65	±1.0672
	" 11	65.65	±1.1256
	" 3	72.65	±1.1113
	" 12	72.65	±1.0745
	" 14	73.05	±1.1055
	" 10	86.25	±1.7644
	" 13	94.05	±1.0460

**Based on 250 measurements; the others each based on 25 measurements.

Mean barbule length in Table 2 given in micrometer spaces, 1 ocular micrometer space equaling 5.2 microns.

of the regular conjugation and divisions in the hybrid itself. Since morphologically as well as cytologically the seedlings qualify as successful backcrosses under natural conditions, a majority of these may have received the more abundant pollen of *L. squarrosa.*

Granted plant No. 52 is a hybrid, the regular pairing in meiosis of the pollen mother cells showed that the chromosomes of the two gametic genomes were homologous. If the chromosomes of the two contributing parents did not differ structurally they would have differed in their genic structure. Two such species which are not reproductively isolated, according to the classification of Mayr (1948), would be but subspecies. Also according to Clausen, Keck and Hiesey (1945), since their genetic systems were so balanced as to allow a free interchange without seriously impairing the ensuing development of the offspring, they would be classified as ecotypes of one species.

It is of interest to note that *L. ligulistylis* and *L. squarrosa* are species of the series *Scariosae* and *Squarrosae.*

On the basis of their barbellate or plumose pappus, Cassini (1827) placed these two series under the sections *Suprago* and *Euliatris,* respectively. Thus × *L. creditonensis* is an intersectional as well as interserial hybrid. Significant evidence of the hybrid origin of × *L. creditonensis* seems to lie in the measurements of the barbules of the pappus of the plants under consideration. As given above, the means of the lengths of barbules of the two putative parents were 30.54 and 92.37 and that of the hybrid was 43.85. Such a value is indeed a near intermediate as is generally found in the F_1 in quantitative characters, and the values of the progeny show recombinations expected in the next generation. It is known that when two pairs of factors affect a character (in multiple factor inheritance) the proportion of the F_2 progeny falling within the range of either parent equals $\frac{1}{16}$. For this one character of pappus, the values in the table suggest that such an interpretation might possibly be considered. *Liatris Weaveri* (Shinners, 1943), though it has not been reproduced experimentally, similiarly appears to represent an intersectional hybrid, between the series *Scariosae* and *Punctatae* (with plumose pappus).

The cytology of × *L. Weaveri* is being treated also (Gaiser, in press I). There are a number of examples in other plant genera of hybrids between what have been considered good allopatric species and even between genera. Therefore, such well recognized forms as *L. squarrosa* and *L. ligulistylis* surely fall into the category of generally recognized good species. Knowing what species were growing in the plot at the time of the appearance of × *L. creditonensis,* it is difficult to see what other parental sources could have given rise to it. Yet the final proof would lie in its experimental resynthesis. Other hybrids of this genus are beirg reported upon (Gaiser, in press II). Of the ten hybrids listed for the genus (Gaiser, 1946) six were intersectional hybrids. Also, in every series of the genus but two, the *Graminifoliae* and *Pauciflorae,* at least some species had been involved in such hybridization (Gaiser, 1950). According to the classification based on biosystematic principles (Clausen, Keck, and Hiesey), the several intersectional hybrids would seem to mean that much of the genus *Liatris* is one cenospecies.

As seen in plant No. 52, × *L. creditonensis* was a sucessful hybrid judged by the achene development and the high percentage of seed germination. The cytological observations foretold this condition in the regularity of meiosis and the formation of regular pollen grains. It was analyzed as a hybrid between *L. squarrosa* var. *glabrata* and *L. ligulistylis,* a hybrid between two species for which there is a natural barrier of geographic isolation. But when these two are brought together, hybridization can result.

TABLE 3. HYBRID INDEX OF PLANT NO. 52 AND ITS PROGENY

	Pilosity on Corolla Limb	Length of Barbules of Pappus	Phyllary			Leaf			Upper Stem	
			Margin	Shape	Position	Shape	Surface	Margin	Pubescence	Total
L. ligulistylis No. 1	0	0	0	0	0	0	0	0	0	0
L. squarrosa var. *glabrata*, No. 32	4	2	2	2	2	2	2	2	2	20
X. *L. creditonensis* No. 52	1	.44	1	1	1	1	2	2	1	10.44
Progeny Plant, of No. 52 1	3	.75	2	2	2	1	2	2	2	16.75
2	3	.44	1	1	1	2	2	2	1	13.44
3	2	1.40	1	1	0	2	2	2	1	12.40
4	3	.49	2	2	2	1	2	2	2	16.49
5	3	1.10	2	2	1	1	2	2	2	16.10
6	4	.17	2	2	2	1	2	2	1	16.17
7	2	.55	2	2	1	1	2	2	1	13.55
8	2	.92	1	2	1	2	2	2	1	13.92
9	2	.81	1	1	0	1	2	2	1	10.81
10	1	1.85	2	2	2	2	2	2	2	16.85
11	3	1.17	2	1	2	1	2	2	1	15.17
12	1	1.40	2	1	1	1	2	2	2	13.40
13	4	2.11	2	2	2	1	2	2	2	19.11
14	4	1.41	2	2	2	1	2	2	2	18.41
15	2	.57	1	1	0	1	2	2	1	10.57

SUMMARY

1. Two species of *Liatris* from different sections of the genus were grown in an experimental garden. A seedling appeared whose intermediacy, vigor, and breeding behavior indicated that it was a first generation hybrid between these two species.

2. There was no evidence of cytological irregularities or of any sterility either in the hybrid or its open-pollinated progeny.

3. Fifteen open-pollinated seedlings of the hybrid were raised to maturity and measured for a series of characters. They are as a whole intermediate between the hybrid and one of the parents, suggesting that wholly or in part they are back-crosses.

4. The concept of the cenospecies, as applied to *Liatris,* is discussed in the light of these results.

Biological Laboratories,
Harvard University,
Cambridge, Massachusetts

LITERATURE CITED

ANDERSON, E. 1949. Introgressive hybridization. John Wiley & Sons. 109 pp.

CASSINI, A. H. 1827. Dictionnaire des Sciences Naturelles 51: 384.

CLAUSEN, J., D. D. KECK, and W. M. HIESEY. 1945. Experimental Studies on the nature of Species II. Plant evolution through amphiploidy and autoploidy with examples from the Madinae. Carnegie Inst. Wash. Publ. 564. 174 pp.

GAISER, L. O. 1946. The genus Liatris. Rhodora 48: 165–183, 216–63, 273–326, 331–82, 393–412.

——————. 1950. Chromosome studies in Liatris II. Graminifoliae and Pauciflorae. Am. Jour. Bot. 37: 414–423.

——————. (In press I) A natural hybrid of Liatris (×L. Weaveri Shinners). Am. Midland Nat.

——————. (In press II) Evidence for intersectional field hybrids in Liatris. Evolution.

MAYR, E. 1948. The bearing of the new systematics on genetical problems. The nature of species. Advances in Genetics 2: 205–237.

SHINNERS, L. H. 1943. A revision of the Liatris scariosa complex. Am. Midland Nat. 29: 27–41.

MORTON EATON PECK

Morton Eaton Peck, Professor-Emeritus of Biology at Willamette University and dean of plant taxonomists in the Pacific Northwest, will celebrate his eightieth birthday on March 12, 1951.

Born in La Porte City, Iowa, Dr. Peck received most of his formal academic training at Cornell College (Iowa). After graduation he held several teaching posts in Missouri and Iowa and spent two fruitful years as a botanical collector in British Honduras. In 1908 he came from a professorship at Iowa Wesleyan to Willamette University, Salem, Oregon.

More than half of his eighty years have thus been spent in acquiring an unequaled knowledge of the natural history of

(Photograph by Bishop Moderne Studios)

PLATE 2. MORTON EATON PECK

Oregon and imparting his deep appreciation of it to successive generations of attentive students. Accompanied by his able and devoted collaborator, Jessie Grant Peck, he has done extensive field work in almost every section and corner of the state, on foot, on horseback, and by automobile. His knowledge of the flora of the Wallowa, Steens, and Cascade ranges and their intervening plains is an incomparable one. A few months ago he remarked, a trifle wistfully and with characteristic modesty, "I am beginning to think I have covered the state fairly well." The Peck Herbarium at Willamette University, the finest collection of Oregon plants in existence and almost wholly the results of the Pecks' loving efforts, is a permanent and useful record of their explorations and a hospitable haven for botanical visitors.

Although best known to botanists in general for his excellent "Manual of the Higher Plants of Oregon" (1941), Dr. Peck has also contributed pioneer work on myxomycetes (1932), is the author of a distinguished "Preliminary Sketch of the Plant Regions of Oregon" (1925), and has published one book of poems. Currently, he is busily at work on a revised edition of his manual.

We take this opportunity to congratulate him upon his outstanding accomplishments and to wish him many more happy and productive years. Lincoln Constance, Department of Botany, University of California, Berkeley.

REVIEWS

Principles of Plant Infection. Ernst Gäumann, xvi + 543 pages, 311 figures and 90 tables. $8.00. Hafner Publishing Company. New York, New York. 1950. (Authorized English edition by William B. Brierley, Professor of Agricultural Botany in the University of Reading, England.)

This book is a translation of "Pflanzliche Infektionslehre,"[1] first published in 1946. It is therefore not a new book, and earlier reviews should be considered. Among these is one by the translator and editor, William B. Brierley[2] that especially deserves reading, for in it one finds the key to the excellence of the present volume. Professor Brierley has done much more than translate with fidelity the contents of a book; he has succeeded in translating the author of that book as well and to such perfection that when one reads the various chapters in it one seems actually to hear Professor Gäumann deliver his inspiring lectures in the English language.

---

[1] Gäumann, Ernst. Pflanzliche Infektionslehre. Verlag Birkhäuser, Basel, Switzerland.

[2] Brierley, William B. Pflanzliche Infektionslehre. By Ernst Gäumann. Pp. 611 with 311 text-figures and 90 tables in the text. Basel, Switzerland: Verlag Birkhäuser. 1946. S.Fr. 48–50. Annals of Applied Biology 33: 336–337, 1946.

The appendix to the book, written by Professor Brierley (pages 498–513) is excellent but too brief. However, even in its brevity, it leads one to wonder why these two recognized scientists, Gäumann and Brierley, did not, for the sake of effectiveness and efficiency, get together and produce an entirely new and up-to-date book in which the most significant of later biological researches and ideas could be included.

The book appears to be exceptionally free of errors. This reviewer was able to find only one of serious import, and that one was probably due to the obvious attempt at effecting economy in space and materials. The error occurs on pages 476 and 481 where the graphs, but not the legends, of figures 306 and 311 have been transposed. Also in the text are two references, with dates, which are not found under literature cited.

The book is divided into six chapters, and these are further divided under subheadings into many categories that help to systematize and clarify their content.

Chapter 1 deals with the mechanisms of infection used by the various pathogens, phanerogams, fungi, bacteria and viruses, and shows how these are influenced by environmental conditions. Also discussed are the various paths and portals through which pathogens enter and their further development and colonization within the host.

In Chapter 2, infection chains are considered, as well as the many kinds and sources of infective materials. The manner in which these differ for autoecious and heteroecious pathogens likewise is discussed. Also considered here is the way infection chains affect the start, development and decline of epidemic outbreaks of infectious plant diseases.

Chapter 3 is concerned with the adaptive ability of pathogens. In it are discussed in some detail the kinds and degrees of pathogenicity that can be brought about by such factors as nuclear dissociation (saltation), nuclear association (heterocaryosis), hybridization, and mutation. Here, also, is brought in a discussion of the effectiveness of mixed infections of different strains of the same pathogen and mixtures of different species of pathogens.

Chapter 4 deals entirely with the host and its proneness, its susceptibility or its resistance, to disease. The chapter is divided into two parts. First is discussed the inherent resistance of the host to infection, penetration and internal spread of the pathogens, with some 65 pages devoted to consideration of the many defense reactions of the host. Secondly is considered the changes in resistance due to such factors as ontogenetic changes in the host, general vigour of the host and the effects of the physical environment, temperature, humidity, etc., including the agricultural activities of man.

In Chapter 5 is discussed the pathological effects of the interactions of host and pathogen resulting in many kinds of symptom expression. In Chapter 6 the various prophylactic and therapeutic means of plant disease control are treated.

Principles of Plant Infection is a good book, a stimulating book with interpretations here and there that can and will be questioned and reconsidered by students of Plant Pathology—H. N. Hansen, Division of Plant Pathology, University of California, Berkeley.

Plants of Bikini and Other Northern Marshall Islands. By William Randolph Taylor. The University of Michigan Press, Ann Arbor, Michigan. xv + 1–227 pp., frontispiece, plates 1–79. 1950. $5.50.

As a senior biologist of the technical staff attached to the atomic-bomb tests of "Operation Crossroads," it was the responsibility of Professor Taylor to collect and catalogue the plants, with the exception of the phytoplankton and bacteria, that occur on the Atolls of Eniwetok, Bikini, Rongelap, and Rongerik.

Among those interested in the botany of the Pacific, it is well known that little information exists about the floras of many of the island groups in this large ocean. With respect to the northern Marshall Islands the situation was particularly bad, for, as the author points out, there was almost no background at all for a botanical survey—nothing was known of the cryptogamic floras.

The subject matter is treated under five main headings: In part one (pp. 1–4) the history of botanical exploration in the Marshall Islands as a group is briefly reviewed. In part two (pp. 5–13) the appearance and structure of the atolls is described, and a general account is given of the marine vegetation and the ecological conditions as encountered on the seaward reefs and in the lagoons. It is of interest to note that such ubiquitous tropical genera as *Sargassum* and *Galaxaura* are entirely absent and others such as *Codium* and *Dictyota* are very poorly represented. The vegetation of the seaward reefs is totally different from that in the lagoons. In both areas the littoral and upper sublittoral vegetation is extremely poorly developed, apparently owing to the intense insolation. Lithothamnioid algae, chiefly of the genus *Porolithon,* are the most important elements in the growth of the windward (eastern) side of the reefs and are of great importance in reef formation on the leeward side of the atolls also.

Part three (pp. 14–18) deals with the general characteristics of the land vegetation. It is pointed out (p. 14) that: "The land flora of the four atolls is essentially uniform. There are no differences with respect to basic vegetation between any of the atolls, and infrequent and introduced wild species nowhere alter the botanical aspect of an island." In part four (pp. 19–39) a more detailed summary account is given of the islands (more than 50 were visited) in each of the four atolls.

Part five (pp. 40–209) consists of an annotated catalogue of the plants. The Latin diagnoses of the new species are assembled at the end of this section. Descriptions are provided for about 250 species, varieties, and forms (56 angiosperms, 1 moss, 11 fungi, and the remainder algae, all of which are marine in occurrence except for a few Cyanophyceae). Seventeen species and forms of algae and four species of fungi are regarded as new to science.

In the identification of the species, Professor Taylor had the assistance of various experts. However, except for the blue-green algae, the fungi, and a few other species, the task of drawing up the descriptions fell on his shoulders. The masterly way in which this was done is proof of Professor Taylor's versatility as a botanist.

Descriptions are furnished only for the species, varieties, and forms. Many of them are illustrated with photographs of the habit. In the majority of instances, the photograph of the habit clearly reveals the outstanding features of the entity but in others, such as *Halimeda,* it would have been extremely helpful if anatomical details had also been illustrated, as they were in some of the Corallinaceae. In most instances, except for the angiosperms, the date of publication of the genus is given. One wonders why this was not done for the species also, and it is especially to be regretted that in many instances the reference to the species or the forms with which they are compared (e.g., *Haloplegma Duperreyi* subsp. *spinulosum* Howe, p. 138) was not given in the bibliography. The citation of this essential literature would have enhanced the value of the book and would not have increased its bulk by more than a few pages. On the other hand, a few of the references which are given, such as those of Børgesen on *Rosenvingia stellata* (now *Iyengaria stellata* (Børg.) Børg.) and *Platysiphonia,* could safely have been omitted since they are not particularly relevant.

For several genera, a wrong date of publication is given. In the following list the year of publication is that given in parentheses: *Cladophoropsis* Børgesen, 1909 (1905); *Microdictyon* Decaisne, 1839 (1841); *Acetabularia* Lamouroux, 1816 (1812); *Tydemania* Weber-van Bosse, 1911 (1901); *Spermothamnion* Areschoug, 1877 (1847).

Inasmuch as the author alone is responsible for the greater part of the account dealing with the marine algae and since this is the group with which the reviewer is most familiar, a few critical comments may be appropriate.

Despite the convincing arguments of Børgesen, Feldmann, and others for the separation of the members of the Siphonocladales into several families, Professor Taylor still places *Valonia, Val-*

oniopsis, Dictyosphaeria, Cladophoropsis, Boodlea, Rhipidiphyllon, and *Microdictyon* in the single family Valoniaceae. Børgesen and others would assign only *Valonia* and *Dictyosphaeria* to the Valoniaceae.

Notice has apparently not been taken of the fact that *Valonia Forbesii* has been made the type of a distinct genus independently by Feldmann (C. R. Acad. Sci. Paris 206: 1504. May 1938, as *Boergesenia*) and Iyengar (Jour. Indian Bot. Soc. 17: 194. June 1938, as *Pseudovalonia*).

In discussing the new species, *Caulerpa bikinensis,* the author remarks (p. 66): "Difficult though the [*Caulerpa racemosa*] group is, one can clearly recognize certain lines of specialization and these lines deserve species rank, understanding that, where conditions do not favor the full expression of the differences to which a plant has genetically attained, recapitulation may cause simpler ramellar forms to be exhibited. Examples would include *C. peltata* and *C. bikinensis,* . . ." This view is at variance with that taken by Eubank (Univ. Calif. Publ. Bot. 18: 409–432. 1946.) in her study of the Hawaiian species of *Caulerpa.* On the basis of her own observations and those of other investigators of *C. peltata,* she concluded that this entity intergraded to such a perplexing degree with variants of *C. racemosa* that it was not possible to accord it more than varietal status. In the absence of experimental evidence it is futile to argue for or against recognition of *C. peltata* and various other entities of *Caulerpa* as species, varieties, or forms, except that it is more in keeping with current practice to consider them as intergrading variants of polymorphic species.

It is not clear whether or not the author regards all members of the Fucales as belonging to a single family. *Turbinaria* is assigned to the Fucaceae whereas most modern systematists give it a place in the Sargassaceae.

Botryocladia Kuckuckii is considered by Feldmann (and more recently by Børgesen) as synonymous with the older *B. Skottsbergii.* The author adopts the former name for the plant from Bikini without giving his reasons for differing from Feldmann.

Inasmuch as the families and genera are arranged in phylogenetic sequence in the groups to which they belong, it would have been more logical to place *Laurencia* and *Chondria* at the end instead of the beginning of the Rhodomelaceae.

In general, the nomenclature is up-to-date. The following are a few oversights to which attention may be drawn.

The transfer of *Asperococcus fastigiatus* Zanardini to *Rosenvingia* was made by Børgesen when he established the genus.

Acrochaetium is placed in the Chantransiaceae, but since it is now known that *Chantransia* as originally conceived did not include members of *Acrochaetium* or related genera there is no longer justification for failure to accept the family name Acrochaetiaceae.

The authors and dates of publication of *Neomeris* ("D'Archiac, 1843"), *Hypnea* ("Kützing, 1813"), and *Ceramium* ("Wiggers, 1817") are Lamouroux, 1816, Lamouroux, 1813, and Lyngbye, 1819, respectively. Wiggers did, to be sure, describe a genus *Ceramium* in 1780, but his genus was founded upon species of *Chorda, Furcellaria,* and *Gracilaria,* and did not include a single species of *Ceramium* in the sense that the genus is now accepted. *Ceramium* Lyngbye has been conserved.

The name *Roschera* Sonder (1879) should be supplanted by *Tolypiocladia* Schmitz (1897), since this name of Sonder is an orthographic variant of *Roscheria* Wendl. (1877), a palm genus. Both names commemorate Dr. Albrecht Roscher.

Although the flora of the northern Marshall Islands is not a rich one, the volume by Professor Taylor forms a most gratifying and welcome addition to organized knowledge of the marine algae of the Pacific. We now have for the first time a book giving good descriptions of some of the algae which students visiting the central Pacific could expect to find.

The University of Michigan Press has maintained its usual high standard in the printing and binding of the volume.—George F. Papenfuss, Department of Botany, University of California, Berkeley.

Anatomy of the Dicotyledons. By C. R. Metcalf and L. Chalk. Oxford at the Clarendon Press. Volume I, i–lxiv + 1–724 pp., Volume II, 725–1500 pp., 1950. $25.00.

In 1899 Solereder published his Systematic Anatomy of the Dicotyledons. This work resulted from a venture begun by Radlkofer and pursued further by his students, which sought evidence for the interrelationships between plants from the details of their anatomy. Solereder summarized the accumulated knowledge in the two volumes of his treatise. Since then many new facts have become available, necessitating some corrections in old observations. Metcalf and Chalk have attempted to bring all this material up to date, at the same time laying further stress on its relationships to Taxonomy. The present review will stress the taxonomic aspects of the work.

The preface outlines the authors' aims and objectives, while the introduction presents a resumé of generalizations as to the rôle of Plant Anatomy in Taxonomy. The body of the text outlines factual material relative to each family's normal and anomalous anatomical features, with additional phylogenetic, taxonomic, and economic notes, followed by lists of genera from which the factual data is derived, and, finally, pertinent bibliographic references. At the end of the work are interesting lists of plant families, each list exhibiting certain anatomical characters in common. This is followed by lists of families having similar patterns of geographic distribution and, finally, lists of various woody or herbaceous families. The appendix contains six tables pertaining to measurements or counts of vessels, rays or fibers. The work closes with a general bibliography of 2535 entries, most of which are subsequent to Solereder.

The taxonomist will be interested in the arrangement of the families, which follows the system of Bentham and Hooker, and he will naturally attempt to seek the authors' reasons for using this system instead of a more modern, putatively phylogenetic system. The answer will be found on page lv of the introduction and is no more profound than, "On the advice of Sir Arthur Hill, who was director at Kew when the work was started. . . . " Modern usage, however, is followed in the families recognized, approximately 100 family names not included in Bentham and Hooker are used, and the sequence of a few has been changed. Aside from the fact that Solereder, after whom the present work is patterned, also uses the Bentham and Hooker arrangment, there are perfectly sound reasons why such a system may be used in a modern work designed to support phylogenetic taxonomy. Although it was not intended as a phylogenetic system, the principles that guided Bentham and Hooker in developing their "natural arrangement" were based upon morphological resemblances as indicators of "affinities". These are the same principles used in the erection of phylogenetic systems. The only important difference between a natural and a putatively phylogenetic arrangement is that the latter presumes an understanding of the meaning of relationship or affinity. Relative to the Dicotyledons, the systems of Jussieu, of Bentham and Hooker, and of Bessey are very much alike, the differences between them being largely due to additional factual material rather than to basic arrangement.

I am therefore somewhat disturbed by the frequent use of the terms Taxonomy and Phylogeny by the authors in the sense that the former stands solely for relationship on the static level of "affinity", while the latter seeks to establish evolutionary sequences between the families of plants. There seems to be no realization by the authors that the evidence for the former is precisely the evidence for the latter, and that things equal to the same thing are thus themselves equal. Phylogenetic classifications are not ultimate things apart from systems expressing affinity. In Taxonomy, phylogeny as yet can only be an enlightened point of view that governs or limits and guides the use of the concept of affinity in making taxonomic arrangements, for there are no means whereby the precise course of genetic lineages can now be established. They belong to the irretrievable past. Yet we believe that the plants within the inclusive taxonomic structure that constitutes our orders and families and our genera and species typify segments of the phylogenetic lineage. We believe that these lineages, through genetic processes, have been characterized by modifications of the details of morphological structures. Today the precise concepts of affinity become a part of the phylogenetic classification which stands as the working hypothesis of the taxonomist. That is about as far as we can go, but it is important that we go that far. The system thereby achieved lends itself to many important uses such as the education of botanists, and the more practical problems of the identification of plants, the selection of grafting stock, and the seeking of additional or substitute sources of the products of biochemical synthesis.

The authors reach the conclusion that some families are anatomically homogeneous and therefore probably natural, while others are heterogeneous and hence may be unnatural and should be reinvestigated. They maintain that anatomical features are most likely to provide evidence of the interrelationships of family and larger groups, that they may also help establish the real affinities of uncertain genera, but that they are of little value on the species level. They also touch the age-old problem of the evaluation of characters, and they emerge with a reexpression of the doctrine of conservative characters, suggesting that the taxonomic value of anatomical characters is inversely proportionate to their plasticity and that conclusions based on combinations of characters are more reliable than those resting on single characters. They point out that the possession of similar anatomical features does not always imply affinity, and that anatomical features of value in one family are not necessarily of value in another. These same principles were established for organography by Jussieu, DeCandolle, and Bentham and Hooker. Thus in the evaluation of characters for taxonomic purposes Plant Anatomy finds itself in a similar situation with the other systematic disciplines.

I sought to discover if the work might be utilized to determine whether a family suspected of being unnatural on other grounds might also be found unnatural on the basis of its anatomy. For this purpose I selected the Ficoidaceae (Aizoaceae). Here the embryo in one group of genera is shaped like the letter "C", suggesting relationships with the Caryophyllaceae, while another section of the family has an embryo shaped like the letter "L", suggesting relationship with the Cactaceae as is supported by other features of gross morphology. Maheshwari in his text on Plant Embryology noted the resemblance of Cactaceae to Ficoidaceae and concluded that Cactaceae should be placed close to Caryophyllaceae. I sought to determine if the anatomical facts might not warrant splitting Ficoidaceae, one group remaining close to the Caryophyllaceae, and the other placed near the Cactaceae. The coverage of this family in the text under review, however, was not adequate to make such a comparison, and I was unable to reach my own conclusion in this matter. It would seem that the value of the book to the taxonomist is directly in proportion to the completeness of detail in which the families are treated. I am fully aware that this is probably expecting far more of the work than was intended by its authors, since the organization presented centers around the family rather than the genus. To cover the genera adequately would require a treatment encyclopedic in scope. Nevertheless I think my point is worth making. It would seem that in order to evaluate adequately the relationships of a family one must understand its organization into genera inasmuch as it is the generic characters that suggest the phylogenetic lineages of the family.

In the closing sentence of the treatment of the Ficoidaceae the authors state that, "A complete anatomical revision of the family could usefully be undertaken as soon as the taxonomy of the family is more stable." Plant Anatomy will be of greatest service to Taxonomy when from its own evidence it ventures its own conclusions and erects its own hypotheses concerning phylogenetic matters. Only in this way can we get a systematic viewpoint not biased by evidence from other disciplines. Only in this way can we pit the evidence and conclusions of one discipline against those of another to test hypotheses of relationship. Obviously the conservativeness of anatomical characters does not permit this on the scale upon which some of the other disciplines operate. Nevertheless, it seems important that as much independence of decision as possible enter the work.

There are at present only a few families whose anatomical features have been studied systematically to the point of maximum use to the taxonomist. Such studies require time and hard work and involve the massing of materials from remote places. It is of immense value that after each fifty years of progress the material be brought together where it may be assimilated. This Metcalf and Chalk have done in fine style. It has been my objective to point out places where a closer tie could be woven between Plant Anatomy and Taxonomy. This is especially important because Taxonomy is at present undergoing a reorganization and a re-evaluation of its concepts, and it is to this reorganization that much of my present discussion is directed. Toward this objective these volumes are a monument of achievement such as few men complete in a lifetime. The task is Herculean and each generation of plant anatomists and plant taxonomists must contribute its mite. **Herbert L. Mason**, Department of Botany, University of California, Berkeley.